

THE MOTHER-OFFSPRING RELATIONSHIP OF SOME BLABERID
COCKROACHES (DICTYOPTERA: BLATTARIA: BLABERIDAE)

LOUIS M. ROTH

U.S. Army Research and Development Command, Natick, Massachusetts 01760; send correspondence to: 81 Brush Hill Road, Sherborn, Massachusetts 01770.

Abstract.—Nymphs of the ovoviviparous cockroach *Perisphaerus* sp. cling to the undersurface of the mother for at least two instars. These small nymphs are blind and have specialized, non-chewing-type mouthparts. The latter suggests that the nymphs obtain nourishment from the mother, or possibly from plant tissue. If the former is true, then the apophyses, to which muscles are attached and which open externally between the mid- and hindcoxae, may have evolved a secondary function of producing nourishment for the immatures.

What little is known about the mother-offspring relationship of *Perisphaerus* is based almost entirely on data associated with pinned museum specimens. Observations on living material are needed to elucidate the maternal and nymphal behavior of this interesting genus of subsocial insects.

Observations on several species of ovoviviparous Blaberidae suggest a close postparturient relationship between females and their offspring (Roth and Willis, 1960; Liechti and Bell, 1975). A female *Phlebonotus pallens* (Serville) from Ceylon, for example, was found with young cockroaches moving about under her tegmina, on the upper surface of her abdomen. This female cannot fly because her wings are greatly reduced. Her tegmina are large and arched, however, and the upper surface of her abdomen is depressed with its sides raised, forming a chamber in which the new-born can be carried about (Shelford, 1906). A female of this species carrying more than a dozen nymphs was collected in south India; the young were packed so neatly that it was impossible to detect them, and they did not interfere with the activities of the mother. This appears to be a good method for protecting young and dispersing the species (Pruthi, 1933).

Arched tegmina also are found in the closely related genera *Thorax* Sausure and *Phoraspis* Serville, and perhaps these cockroaches too show maternal care. At the slightest alarm the young of some species of "phoras-

pidinae" creep under the dome-shaped tegmina of the mother (Karny, 1925). In her 1964 classification, McKittrick included two of these genera in the Epilamprinae, tribes Thoracini (*Thorax*) and Audreini (*Phoraspis*). In 1972 I placed *Phoraspis* in the Phoraspidini and *Thorax* in the Thoracini.

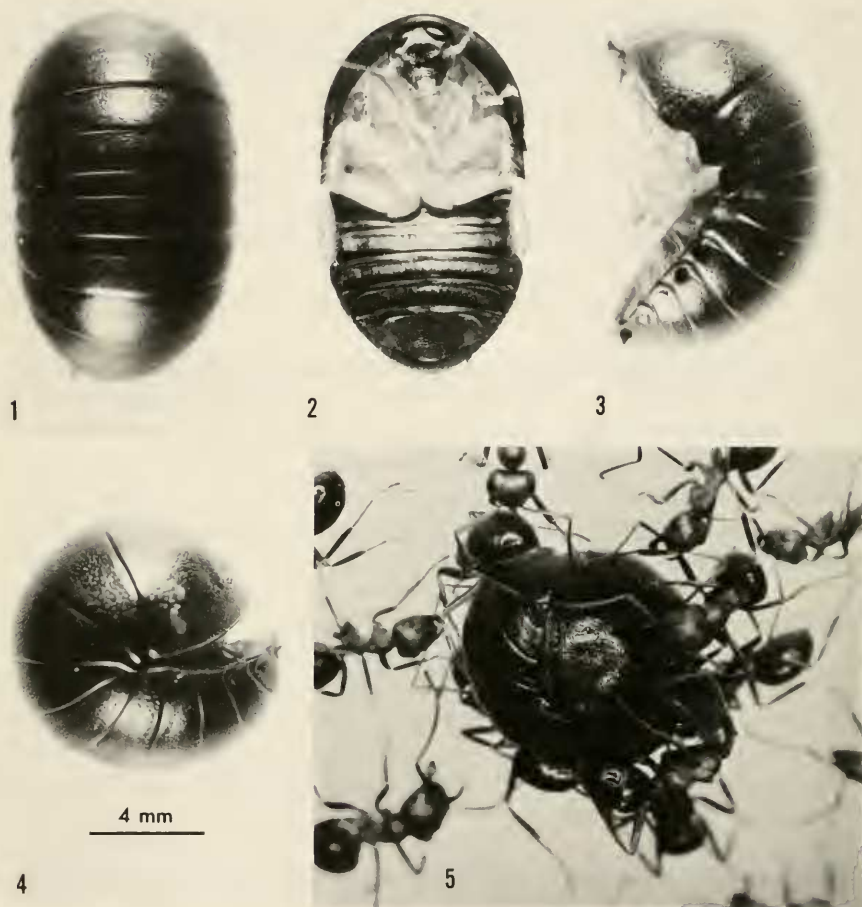
In Luzon in the Philippines, collectors have found the apterous female of *Perisphaerus glomeriformis* Lucas (Perisphaeriinae) with nymphs clinging to her undersurface (Hanitsch, 1933); a similar behavior was reported in nymphs of *Pseudophoraspis nebulosa* (Burmeister) from Borneo (Shelford, 1906). In a brief abstract Gurney (1954) reported that the nymphs of *Perisphaerus* sp. are born alive and cling to the lower side of the mother's body, "The head of the first instar nymph has a very elongate face and slender specialized galeae."

In 1968 Noel Kobayashi sent me four living females of *Perisphaerus semilunatus* (Hanitsch) from Sakaerat, Khorat Province, Thailand. When disturbed the apterous females roll up into spherical balls that resemble pillbugs because of their convex form and shiny black color (Figs. 1-4). It is unknown whether species of this genus are distasteful to predators, and it is doubtful that they mimic a particular species of pillbug (Shelford, 1912). In the ball position, however, they are protected from invertebrate predators by their hard integument. These insects have become so modified morphologically that, rolled up, the edges of the pro-, meso-, and metanotum meet and fit tightly against the edges of the abdominal terga. Females of *P. semilunatus* roll up so tightly when handled that it is almost impossible to straighten them out without damaging their cuticles. All of the vulnerable structures of a rolled-up female are completely hidden, insuring her safety from the attacks of ants (Fig. 5; Eisner, personal communication). Sexual dimorphism is outstanding, the males are fully winged and do not roll up in a ball.

Ball-forming behavior, which probably evolved independently in cockroaches and millipedes (Shelford, 1912), may be nothing more than an exaggeration of a reflex common to many cockroaches, i.e., the arched position these insects assume when they immobilize themselves in response to certain stimuli (Chopard, 1938).

Recently I examined some of the specimens of *Perisphaerus* sp. mentioned briefly by Gurney (1954). I believe that information can be added to the little we know about the mother-offspring relationship. Among the specimens in the U.S. National Museum, two females had been dissected, and all nymphs detached from their mothers and mounted on slides or pins, or their heads had been placed in glass tubes. The adult females (Figs. 6, 8) in the collection bear the following information on labels associated with the specimens:

1. Mindanao, Davao Province, Mt. Galintan, May 1927, R. C. McGregor.
"Perisphaerus female with 9 young among legs when rolled up like a *Glom-*



Figs. 1-5. *Perisphaerus semilunatus*, female from Thailand. 1, Dorsal, 2, Ventral, 3, Lateral, 4, Lateral and rolled up in ball position. 5, Rolled up and being attacked by ants.

eris; 1 young left with specialized mouthparts in intercoxal gland orifice . . . H. S. Barber, 1931." (The last mentioned nymph apparently had been removed by a later examiner.)

2. Surigao, Mindanao, Baker. "*Perisphaerus* female with 1 young clinging to middle coxa—no ootheca . . . H.S.B., 14.v.1931."

3. Mt. Makiling, Luzon, Baker. "Egg mass from cavity in abdomen lost . . . 3 young clinging to coxae."

4. Sibuyan Island, Baker. "*Perisphaerus* female with 1 broken youngster between mid and post coxae—removed and mounted in 2 beads—no eggs in pouch. H.S.B., 15.v.1931."

5. San Pedro, Culion Is., P. I. (Calamianes Group); nr. sea level,

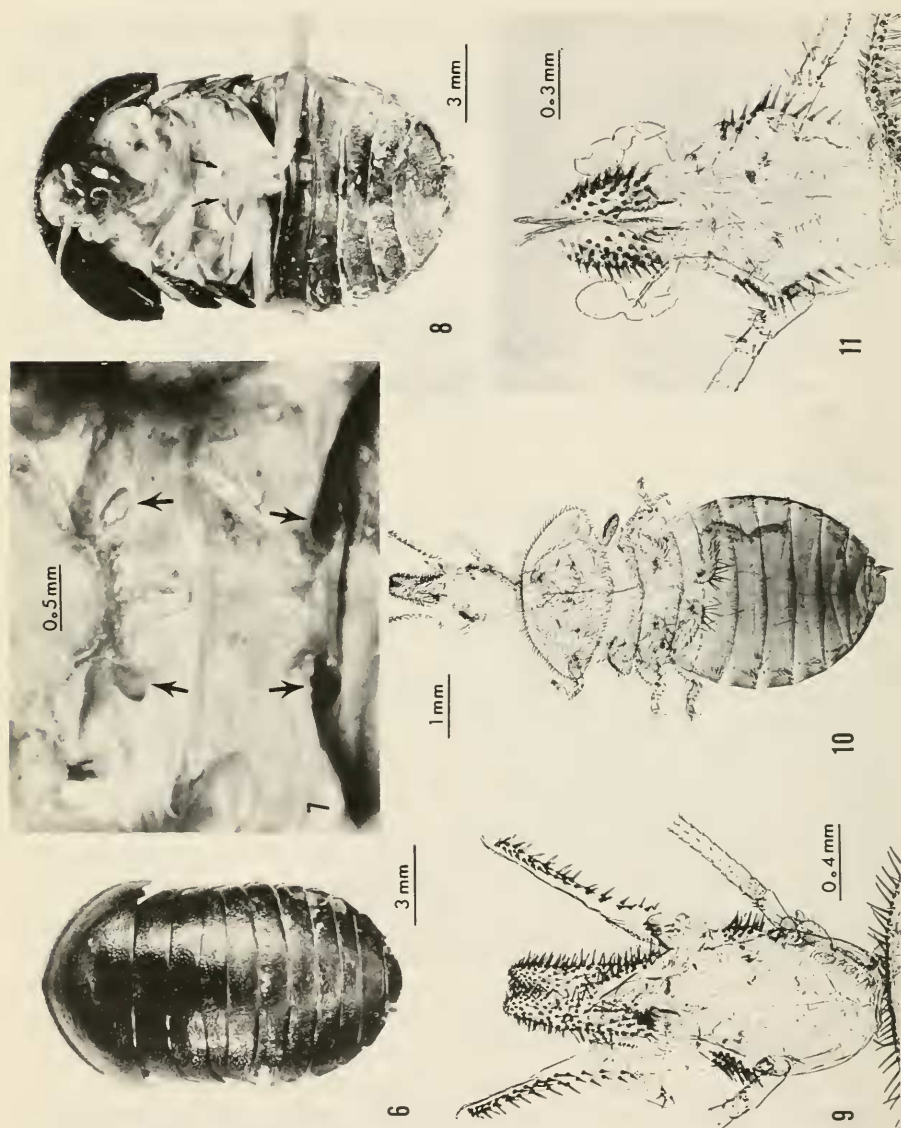
29.iii.1947. CNHM (=Chicago Natural History Museum) Philippine Zool. Exp. 1946-47, H. Hoogstraal. *Pandanus* Mangrove Zone—In terminal leaf axils of *Pandanus*. 3 nymphs, "cling to underside of female."

These data inspire the following questions: Can nymphs of *Perispbaerus* remain attached to their mother when she rolls herself into a ball, and thereby be protected from potential predators? The information on labels associated with female number one shows that they can, and that at least nine nymphs are able to remain attached when the female assumes the defensive position.

Removing the oothecae from four females (15-16 mm long) collected on the eastern slope of Mt. McKinley, Davao Province, Mindanao, P. I., I found that the respective numbers of eggs in the egg cases were 11, 12, 15, and 16. Three larger females (23 mm long) of a different species from Sibuyan Island had 15, 17, and 18 eggs in their oothecae. Whereas these numbers appear small for an ovoviviparous species, the mother cockroach probably would have a difficult time carrying around even this relatively small number of young for any length of time. Based on differences in mouthpart structures (cf. Figs. 9, 11) nymphs from Mindanao found clinging to the mother, probably stay attached to her through at least two instars. The unusually developed pulvilli (Fig. 12) probably are used by the nymphs for holding on to the female.

The structure of the nymphal head suggests more than a casual mother-nymph relationship, and that it is not simply a case of phoresy. The mouthparts are greatly modified (Figs. 9-11, 12, 13) and in female number one, a nymph had its specialized mouthparts in an "intercoxal gland orifice." The unusual proboscis-like mouthparts (Fig. 12) appear to be adapted for insertion into the holes; the "proboscis" of this nymph is about 0.3 mm wide, which is about the same as the width of the intercoxal openings. One is tempted to suggest that some kind of nourishment is produced by the mother and accumulates in the intercoxal depressions where it is fed upon by the nymphs.

However, the fact that a nymph had its mouthparts in one of the openings may have been accidental and of no significance. There are four distinct orifices (Figs. 7, 8), a pair occurring between the coxae of the mid- and hindlegs; in addition there is a less distinct medial opening between the holes of the midcoxae. Cuticular preparations of the intercoxal areas show that the holes are the openings of elongated apodemes (furcal arms) which are tubular for most of their length, and which extend laterally (Fig. 17). The additional small hole between the midcoxae is a shorter vertical spina. Muscles are attached to these structures, the usual function of apodemes, but whether or not glandular cells are associated with the furcal arms could not be determined from the cuticular (KOH treated) preparations of dried specimens. There were no visible cuticular ducts which one might expect if secretory cells were associated with the organs.



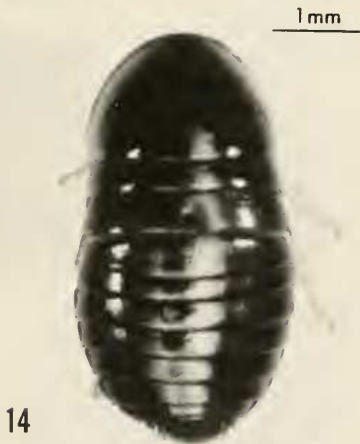
Figs. 6-11. *Perisphaerus* sp. from the Philippines. 6. Adult female from Mt. Galintan, Mindanao (dorsal). 7. Orifices (arrows) of apophyses between mid- and hindcoxae of a female from Mt. Makiling, Luzon. 8. Ventral view of female shown in Fig. 6 (arrows indicate orifices between hindcoxae). 9. Head of nymph shown in Fig. 10. 10. Nymph (probably second-instar) that had been attached to an adult female, 11. Head of nymph (probably first-instar) that had been attached to an adult female. (Figs. 9-11 are chitin preparations).

I examined the intercoxal areas of females of the following ovoviviparous (Blaberidae) cockroaches: *Leucophaea maderae* (Fabricius) (Oxyhaloinae), *Jagrehnia madecassa* (Saussure) (Oxyhaloinae), *Byrsotria fumigata* (Guérin) (Blaberinae), *Eublabeus distant* (Kirby) (Blaberinae), and *Gyna sculpturata* Shelford (Perisphaeriinae). All have large intercoxal apodemes between the mid- and hindcoxae, but they open externally through relatively narrow slits, or do not open externally (openings are represented by narrow grooves, or there are no grooves at all). None have round openings as large (relative to the size of the furcal arms) as those found in the species of *Perisphaerus* I examined. It is possible that in *Perisphaerus*, the intercoxal apodemes not only serve for muscle attachment, but have evolved an additional function.

However, if the nymphs do not obtain nourishment from their mothers, how does one explain their unusual mouthparts? These are not chewing mouthparts typical of cockroaches, and seem to be adapted for obtaining nourishment in some other manner. Perhaps they are inserted into plant tissue, or are used to feed on oozing plant material. If true the nymphs would have to leave the mother, and return to her after feeding. There is evidence that these insects are associated with plants (female number five, and below). Only observations on living or fresh material can resolve these questions.

Not reported previously is the fact that the young nymphs lack eyes which makes them even more dependent on the mother for survival. The stage in which the eyes develop is unknown but, in one species at least, the first two instars are blind (Figs. 9, 11). Three nymphs taken attached to females on Culion Island (number five) may belong to a different species. Two of these (3.8–4.0 mm long) resemble the other immatures (Fig. 10) except that their mouthparts (Figs. 12, 13) are more proboscis-like and lack the numerous setae on the elongated portion; also adult-like mandibles (Fig. 13) are present. They lack eyes, but eyes can be seen beneath the cuticle, and probably the nymphs were near their molting period. A third nymph (4.5 mm long) having similar collection data, taken clinging to the underside of a female, looks like an adult female (Figs. 14, 15). It is darkly sclerotized, has well developed eyes, and adult-like mouthparts (Fig. 16). This specimen may have molted recently, for although it is darkly pigmented, its eyes and head are lighter in color than other similar nymphs. At this stage it is likely that the nymphs no longer depend on the mother and may begin to shift for themselves, although they probably remain gregarious in family groups (see below).

Huber (1976) found that first-instar nymphs of the primitive cockroach *Cryptocercus punctulatus* Scudder, which lives in family groups in rotting logs, are blind, and that the eyes appear in the second-instar as small reddish-brown pigmented structures. The eyes of adult *Cryptocercus* are re-



duced in size, compared to that of other cockroaches, and Huber suggested that reduction in eye size is an adaptation to living in a termite-like niche. In *Perisphaerus* probably the first two instars are blind and the eyes appear suddenly as well-developed structures in a later instar. When the nymphal eyes first appear, they are similar to those of the adult, which are well developed and typical of other cockroaches. The significance of blindness in small *Perisphaerus* nymphs is unknown. Blindness or dramatic reduction of eyes in cockroaches usually is associated with forms that live only in caves (Mackerras, 1967).

From this brief report it is obvious that much can be learned from a study of the maternal care and nymphal behavior shown by *Perisphaerus*. Princis (1964, 1971) lists 17 species of *Perisphaerus*, a genus widely distributed in Asia, Indonesia, New Guinea, the Philippines, and other Pacific Islands. When he collected a species of *Perisphaerus* in the Iron Range on the northern Cape York Peninsula of Australia, Monteith (personal communication) noted that "Most of my specimens have been obtained by beating vegetation, especially when it included dead branches and vines. I recall one occasion when a whole batch, consisting of a couple of adults and many nymphs, came onto the beating sheet at once. This indicates that the adults and immatures are certainly gregarious. Another time I found a number of specimens together inside the hollow rotted out core of some vines hanging from a tree. They also are gotten by beating in New Guinea." Let us hope that this note brings to the attention of biologists a behavior in a group of subsocial insects that is worthy of investigation.

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Figs. 12-17. *Perisphaerus* sp. from the Philippines; 12-16, from Culion Island, nymphs taken clinging to undersurface of mother. 12, Thorax and part of abdomen, ventral view, showing head with its proboscis-like mouthparts, and large tarsal pulvilli (arrow). 13, Chitin preparation of head of a nymph in same stage of development as that shown in Fig. 12 (arrow indicates adult-like mandible). 14, 15, Habitus of an adult-like nymph, dorsal and ventral views, respectively. 16, Head of nymph shown in Fig. 15. 17, Chitin preparation of intercoxal furcal arms of an adult female from Sibuyan Island.

examining large numbers of *Perisphaerus* for the presence of young attached to females.

I thank Thomas Eisner for Figure 5. The late Karlis Princis identified my specimens of *Perisphaerus semilunatus* (Hanitsch) from Thailand.

LITERATURE CITED

- Chopard, L. 1938. La biologie des Orthoptères. *Encycl. Ent., sér. A., Vol., Paris*, 541 pp.
- Gurney, A. B. 1954. [Habits of nymphs of *Perisphaerus*]. *Proc. Entomol. Soc. Wash.* 56: 46. (Abstract)
- Hanitsch, R. 1933. Notes by Dr. R. Hanitsch, Ph.D. on female cockroaches (Blattidae) which carry their young. *Proc. R. Entomol. Soc. Lond.* 8: 18-19.
- Huber, I. 1976. Evolutionary trends in *Cryptocercus punctulatus* (Blattaria: Cryptocercidae). *J. N.Y. Entomol. Soc.* 84: 166-168.
- Karny, H. H. 1925. Een en ander over kakkerlakken (Blattoidea). *De Trop. Natuur* 12: 185-192. (In Dutch)
- Liechti, P. M. and Bell, W. J. 1975. Brooding behavior of the Cuban burrowing cockroach *Byrsotria fumigata* (Blaberidae, Blattaria). *Insectes Soc.* 22: 35-46.
- Mackerras, M. J. 1967. A blind cockroach from caves in the Nullarbor Plain (Blattodea: Blattellidae). *J. Aust. Entomol. Soc.* 6: 39-44.
- McKittrick, F. A. 1964. Evolutionary studies of cockroaches. *Cornell Univ. Agric. Exp. Stn. Mem.* 389: 1-197.
- Princis, K. 1964. *Orthopterorum Catalogus*. M. Beier, ed. Pt. 6, pp. 175-281. W. Junk, The Hague.
- . 1971. *Orthopterorum Catalogus*. M. Beier, ed. Pt. 14, pp. 1041-1224. W. Junk, The Hague.
- Pruthi, H. S. 1933. An interesting case of maternal care in an aquatic cockroach *Phlebonotus pallens* Serv. (Epilamprinae). *Curr. Sci. (Bangalore)* 1: 273.
- Roth, L. M. 1972. The male genitalia of Blattaria. IX. Blaberidae. *Gyna* spp. (Perisphaeriinae), *Phoraspis*, *Thorax*, *Phlebonotus* (Epilamprinae). *Psyche* (Camb. Mass.) 98: 185-217.
- Roth, L. M. and Willis, E. R. 1960. The biotic associations of cockroaches. *Smithson. Misc. Collect.* 141: 1-470.
- Shelford, R. 1906. Studies of the Blattidae. VI. Viviparity amongst the Blattidae. *Trans. Entomol. Soc. Lond.* 1906: 509-514.
- . 1912. Mimicry amongst the Blattidae; with a revision of the genus *Prosoplecta* Sauss., and the description of a new genus. *Proc. Zool. Soc. Lond.* 1912: 358-376.